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NR. 8. Ö. WINGE: ON THE VALUE OF THE RINGS IN THE SCALES OF THE COD AS A MEANS OF AGE DETERMINATION. ILLUSTRATED BY MARKING EXPERIMENTS

KØBENHAVN
I KOMMISSION HOS C. A. REITZEL
BIANCO LUNOS BOGTRYKKERI
1915

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ON THE VALUE

OF

THE RINGS IN THE SCALES OF THE COD

AS A MEANS OF AGE DETERMINATION

ILLUSTRATED BY MARKING EXPERIMENTS

BY

Ö. WINGE

KØBENHAVN
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1. Introduction.

Not until the end of the past and the commencement of the present century did zoologists realise that the scales, otoliths and bones of teleosteans exhibited growth rings analogous to the formations known from stem sections of our trees and bushes. These annual rings were found to be more or less distinctly visible in all the fish examined, a point which naturally could not fail to interest all fishery biologists, for whom reliable determinations of age among such species of fish as are of economical importance must obviously be of the greatest importance.

In the case of several species it has proved possible, in course of time, to secure a good sound basis for determinations of age. This has been arrived at in various ways; for the most part, however, by indirect means, as for instance by investigation of specimens from different seasons of the year, comparisons of otoliths, bones and scales of one and the same individual, and by comparing the results with those obtained by an estimate of the age of younger fish based on the graphical system of measurement. And, as we know, a number of extensive works dealing with empirical determinations of age have already been published. Far less attention has been paid to the experimental side of the question, though it would certainly appear to be of no little importance to prove, if possible, by direct experiment, that the formations in question actually are growth rings. Here, however, we must inevitably encounter serious difficulties, especially in the case of salt-water fish, as it is by no means easy to procure even approximately natural conditions in the small artificial aquaria. It would therefore seem worth while to make the investigation in such a manner as to combine the same with marking experiments, thus using, so to speak, the sea itself as an experimental aquarium. Investigations of this nature may be carried out with several species of fish where scales are used for determination of age. In the present paper, I purpose to confine myself to consideration of the cod (*Gadus callarias L.*).

The experimental investigations hitherto made with gadoids are, as far as we know, but two in number; they are far from complete, and do not agree one with the other. These two experiments may be briefly referred to here:

J. Stuart Thomson[1] mentions having kept a whiting (*Gadus merlangus*) under observation in a small aquarium at the Plymouth Laboratory from shortly after hatching until the fish was 16—17 months old, i. e., from the beginning of May 1902 to 4 July 1903, on which date the whiting jumped out of the aquarium and perished. During this time, it had grown from a length of 10—20 mm to 8.5 inches. On examination of the scales, the writer found that they were far more regular in structure than those of individuals taken in the sea, and he did not observe any formation of growth rings. Thomson remarks that the temperature must be said to have varied but slightly during the experimental period, but would naturally have been colder in

[1] "The Periodic Growth of Scales in Gadidæ as an Index of Age" (Journ. of the Marine Biolog. Assoc., Vol. VII (N. S.), 1904, pp. 1—109).

winter than in summer. As growth zones are also found in fish from deep water, where the temperature does not vary greatly, he presumes that variation in the food obtained is the principal factor in formation of the growth rings.

The second work in which experiments are included, is that of J. T. CUNNINGHAM[1], who examined the scales of some few gadoids which had been used in Dr. T. WEMYSS FULTON's studies in the aquaria of "The Board's Marine Laboratory" at Aberdeen. The results arrived at by this writer may be briefly summarised as follows: a cod and a whiting, living in untemperated aquaria, and a cod kept in an aquarium artificially warmed during the winter, exhibited growth zone formation both in scales and otoliths during the period of experiment. It should be noted, that the writer had no opportunity of examining the original appearance of the scales before the fish were laid down, and that the date of commencement of the experiment was uncertain.

CUNNINGHAM's results are thus mainly in opposition to those of THOMSON.

In 1913 Dr. JOHS. SCHMIDT entrusted me with the task of going more thoroughly into this question, the work to be based upon material consisting of a large number of cod scales collected for the purpose. Now determinations of age are, in the case of the cod, often attended with a considerable element of doubt, owing to the fact that the growth zones of this fish are in the organs referred to generally indistinct. The task before me was thus to ascertain how far it might be feasible, on the basis of the scales and otoliths of marked cod from which scale samples were taken both on marking and on recapture, to decide whether any exact age determination of cod were possible, and whether the peculiar growth rings were due to alteration in external conditions.

The answer to this problem, as furnished by my investigations, will be set forth in the following pages. I have not thought it necessary to refer to earlier works upon the subject beyond the two already mentioned, which are based, like the present, upon actual experiment. The numerous other publications naturally do not and could not furnish any experimental proof that the growth rings in the scales of the cod stand in any relation to the change of the seasons.

I take this opportunity of expressing my thanks to the Head of my Department, Dr. JOHS. SCHMIDT, and to cand. mag. A. STRUBBERG, both of whom have taken an interest in the work, and greatly assisted me in the same with their expert knowledge of the subject.

2. Structure of the Scales of Cod.

A scale taken from the flank of a medium sized cod is found to be a semi-transparent, pliable body, thin as paper, and shaped as a broad, elliptical oval, some 3—4 mm long, and darkly pigmented at its broader end. A magnifying glass of no great power will be sufficient to reveal the fact that the structure is cellular, the cells being arranged in a series of rings, one without the other. The "centre" of the scale is, as a matter of fact, excentrically situated, the rings being drawn about a point lying some little way from the centre of the longitudinal diameter of the ellipse. The cells, moreover, are arranged in radiating rows, the number of which increases outwards, owing to occasional bifurcation. Viewed under the microscope (Plate Fig. 1—2) the cells are seen to be calcareous bodies of characteristic shape; they are known as sclerites, and are easily soluble in dilute hydrochloric acid. The total form is rectangular; each rectangle has, however, parallel with its outermost long side a rounded ridge or roll, which appears to curve in somewhat over the base of the

[1] "Zones of Growth in the Skeletal Structures of Gadidæ and Pleuronectidæ" (23 Ann. Rep. of the Fishery Board for Scotland. For 1904, Pt. III, pp. 125—140).

surface. At the extreme margin of the scale there will always be found an incomplete sclerite ring, which at once shows that the growth is radial.

A microtome section of a piece of cod skin gives a better impression of the structural features, which are here revealed as in Fig. 1. It will be noticed that each scale exhibits a kind of duplicate structure, the inner side consisting of an even fibrous plate which forms the base on which are imposed the calcareous

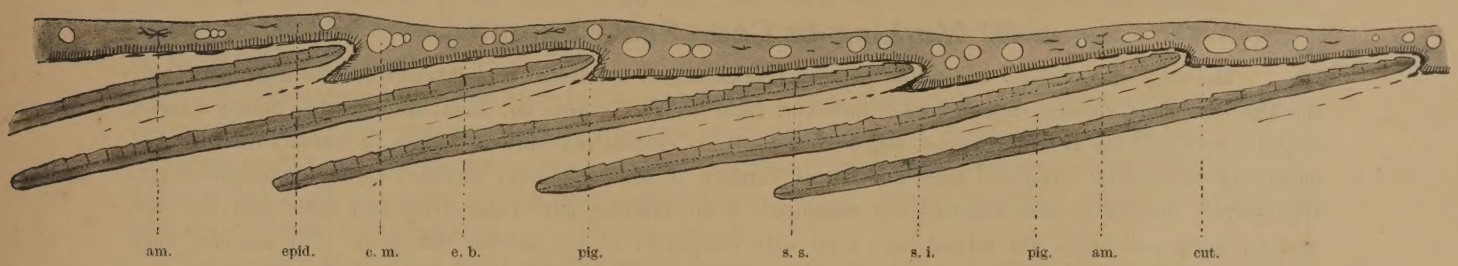


Fig. 1. Horizontal section of a piece of the skin of a cod. Caudal direction to right. *am.* pigmented amœbocytes; *c. m.* mucus cells; *cut.* cuticle; *e. b.* basal cell stratum of epidermis; *epid.* epidermis; *pig.* pigment; *s. i.* inner stratum of scale (base); *s. s.* outer stratum of scale (with sclerites). — From a microtome section, slightly schematized.

processes that form the outer side. This double structure renders it possible, by means of forceps or needle, to divide each scale into two lamellæ. The sclerites vary considerably in shape (Fig. 2), being alternately thick or thin, sometimes with a thick, vaulted ridge, at others with a more sharply prominent edge. Seen in section, we find — as also when viewing the scale from its surface — that the separate calcareous bodies can here and there overlap at the edges, roof-tile fashion (Fig. 2 c). Fig. 1 shows how the scales are set in the skin of the cod. The individual scales are found to overlap, so that each scale observed covers, with its posterior edge, the greater portion of the one behind. Immediately beneath the basal cell stratum of the epidermis, which consists of cylindrical cells, the cuticle is furnished with pigment, which adheres to the posterior edge of a scale when the latter is removed (Plate Fig. 1); this can, however, be easily removed from fresh material, but is more difficult to deal with when dried. The microscope reveals this pigment as in the form of stellate figures, covering the posterior edge of the plated exterior of the scale. Pigment is also found deeper down in the cuticle between the scales, but is here less pronounced. The epidermis is seen to contain branching amoebocytes (a. m.) and large mucus cells (c. m.). The two scale-forming scleroblast strata closely surrounding the upper and lower side of the scales have not been marked in the figure.

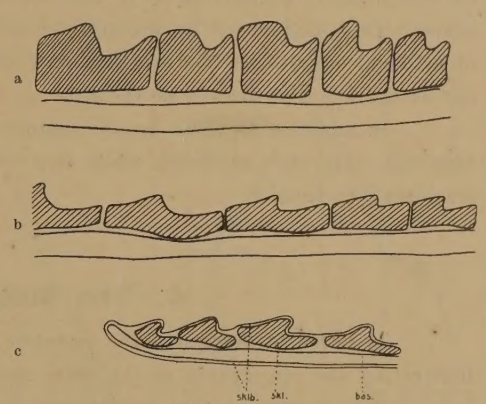


Fig. 2. Portions of longitudinal section of cod scale, showing sclerites of various formation. Caudal direction throughout to left. — *2. a.* scale with very thick sclerites; *2. b.* do. with thinner; *2. c.* margin of scale; *bas.* base of scale; *skl.* sclerites; *sklb.* scleroblast stratum.

The sclerites in a scale are never of equal size, and their radial extent in particular varies greatly. The innermost are as a rule broad, the breadth of those following decreasing until a minimum is reached, when the next increase again in breadth up to a maximum, etc. so that a microscopic inspection of sclerites from the centre out towards the periphery of the scale reveals an alternating succession of minima and maxima. These minima and maxima can be more or less pronounced, and where they are very distinct, each minimum will be visible, even with a magnifying glass, as a darker zone in the scale, somewhat resembling the manner in which the growth rings appear in stem sections of a tree. — It is not surprising that endeavours should have been made to regard the two phenomena as of parallel nature, since it was impossible to imagine any other factor than the change of the

seasons which could be responsible for periodicity in the growth of the scales in cod, from their earliest formation throughout the whole of their developement. On the other hand, many biologists hesitate to accept, without further proof, the theory of annual growth zones in so highly developed animal forms.

3. Marking of Cod. Scale Samples.

The scale material on which the present investigations are based was obtained for the most part from the Faeroes, some portion thereof being, however, from Iceland, where Dr. JOHS. SCHMIDT has during a series of years arranged for the marking of cod with a view to elucidating various points in connection with the biology of the species. The cod were marked on capture in the customary manner, through the gill-cover[1], after having previously been weighed and measured. Scale samples were taken from each individual, the part selected being just above the lateral line, level with the centre of the second dorsal fin. The samples were taken in the following manner: the superficial layer of slime was first removed with the back of a knife; this done, the part in question was scraped several times with the edge, the direction being from tail to head. The scales thus loosened were placed in a small paper bag, marked with the number of the fish, and the latter then set free. On recapture, which took place from 1 to 24 months later, the process was repeated, in addition to which the otoliths were in many cases also removed. Two scales of a cod, taken respectively on first capture and subsequent recapture, are shown in Figs. 1 and 2 on the Plate.

Considerably over half the total number of cod marked were recaptured, most of them after the lapse of only a few months, some, however, not until a year or more later. Strange as it may seem that it should thus be possible to utilise the Atlantic as an aquarium, we cannot but admit the great advantages presented by this method, permitting as it does the normal developement of the fish between marking and recapture, without being influenced by unnatural conditions or any of those disabilities which constantly attend the use of artificial aquaria. — We are here only concerned with such results of the marking experiments as bear on the actual age and growth of the fish.

In addition to these double samples, there were also available various other samples of scales taken from fish only once captured, while live cod from the Danish waters immediately adjacent were purchased from time to time.

4. The Method of Scale Investigation.

In order to determine the essential characteristics of each scale examined, a method for graphically illustrating the appearance of the scale was worked out, with the result that the peculiarities were thus far more distinctly evident than would have been the case with any estimate of these formed by mere microscopical observation. The method is based on measurement of the breadth of the separate sclerite rings in the scale, and will be further described in the following.

A microscope stand with mechanical stage and ocular micrometer, and an objective having a focal diameter of about 8 mm form, as far as my experience goes, the best combination. Zeiss' apochromat: 8 mm, and compensating ocular: 6, with micrometer, giving together a magnifying power of about 185, are excellently suited to this purpose. In addition, it is advisable to have a less powerful objective for preliminary examination of the preparation. One or more scales — fresh scales are especially suitable on account of their transparency — are placed on the object glass, their longitudinal axis about parallel with the longitudinal direction of the object glass itself, the side on which the pigmentation is most distinctly visible being placed

[1] *Vide* JOHS. SCHMIDT: Meddel. fra Kommissionen for Havundersøgelser, Serie Fiskeri, Bind II, No. 6, 1907.

upwards. The micrometer is turned so as to fall parallel with the scales. These are best examined in distilled water, to which may be added a small quantity of potassium hydrate; glycerine and various other liquids are less favourable in point of refraction. Before commencing the examination, the scales may be treated for some time with peroxide of hydrogen solution, whereby the pigment is bleached and finally dissolved altogether; this process, however, generally takes too long, demanding several days, and is, moreover, only exceptionally necessary, as it will often be possible, even with dried scales, to remove the pigment by mechanical means after moistening. Finally, a cover glass is placed over the scales, and the object glass is placed on the mechanical stage.

A well adapted scale will have in the centre only a very small area, the size of some few sclerites, apparently smooth and free from cellular structure: this surface is, as a matter of fact, formed by fusion of the basal portions of the innermost sclerites, as will be seen from specially successful preparations. As a rule, however, there will be several with a large central field devoid of cellular structure; these are regenerated scales, and should be disregarded.

In order to obtain a curve for one of the scales, the instrument is focussed to the centre of the one selected, and all sclerites in the longest radius of the scale then measured, or better, all those in a radius running close outside the pigmented part, by choosing which, the pigmentation will afford no hindrance to the observations. It is of little consequence which radius be taken. In the first place, the most important feature is the proportion between the width of the successive sclerites, and in the second, there is but very little difference between the dimensions of the plates situated on the longest radius and of those on any other radius in the vicinity of this (less than about 20° away). The breadth of the innermost sclerite is frequently difficult to determine, the limit of its basal plate being, as already mentioned, indistinct. This is, however, of no importance. The outermost sclerite, which is not fully formed, is not taken into consideration.

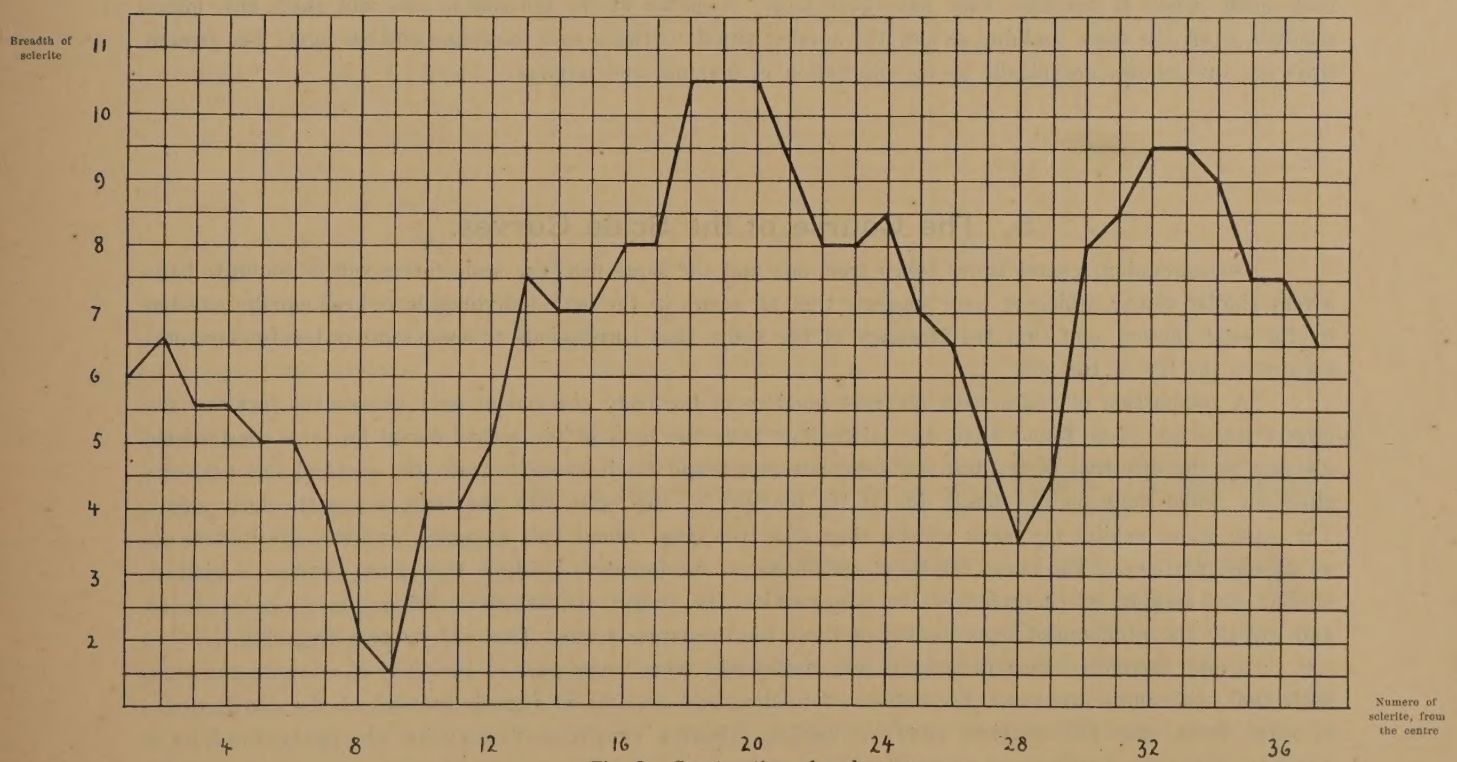


Fig. 3. Construction of scale curve.

The absolute value selected as unit of measurement is naturally of minor importance; I have found it most practical to take for this purpose the interval between the degrees marked on the micrometer itself. With the optical conditions stated above, the distance between each two degrees of the scale of measurement will be about = 8 μ, which figure is therefore taken as unit in the following.

In measuring the sclerites of a radius, the mechanical stage is very useful, rendering it possible to move the object evenly along a parallel line, and ensuring against the accidental omission of one or more interjacent sclerites, which may very easily occur when the glass is moved by hand. In addition, the observer can, with the mechanical stage, better note down his measurement, as no harm is done by losing sight of the preparation. Where this practical aid is not available, the measurements should preferably be dictated to an assistant. In measuring, the dimensions are estimated to the nearest half unit; in case of doubt, the figure nearest that of the last measurement should be taken. Now and again it may happen that a peculiar break in the continuity of the measurements is observed, suggesting the presence of some purely local irregularity. A glance at the adjacent plates in the same sclerite ring will then easily suffice to show whether the sclerite in question is a deviation from the characteristic, and interpolation may then — and only then — be resorted to. If measurement is hindered by the accidental occurrence of particles of tissue, air bubbles, etc. it may without risk be resumed along an adjacent series.

In order to provide a survey of the values thus obtained, the units are noted down on square-ruled paper having an interval of 5 mm between the lines (Fig. 3). A horizontal axis is drawn, from which the measurements of the calcareous plates are marked off in a perpendicular direction, one by one, against each perpendicular line on the paper, each unit being reckoned as 10 mm. On joining up the points thus obtained by straight lines, a curve is produced, which gives a distinct view of the variations in the breadth of the sclerite rings from the centre of the scale towards its periphery. Where the curve is low, the sclerites have been small; where it lies high, they have been large. A glance at the horizontal axis will show how many sclerites in all the scale contains, as also the number situate between each minimum and the next. The growth rings are thus shown graphically as an alternation of maxima and minima.

5. The Course of the Scale Curves.

On examining several scales taken from one and the same fish, the scale curves will be found to have a very similar course, which at once suggests that all scales in the same individual have been equally affected by the same factors, and that the structure of the scales thus corresponds to some more or less fundamental feature in the life of the cod.

A comparison of scales from different portions of the body of a cod at once reveals the fact that the largest scales are to be found along the lateral line from the level of the second dorsal fin for a considerable distance in the direction of the tail: smaller scales are found for instance beneath the pectoral fins near the gill-cover, while those on the dorsal side at the juncture of the head with the body are particularly small. The small scales exhibit far fewer sclerite rings than the large, about half as many, and the sclerites are on an average narrower. The curve for these will, however, be found to contain the same number of distinct minima and maxima as characterised the larger scales, the course of the curve being a somewhat reduced and slightly less pronounced reproduction of those for the larger scales. This will be seen from Fig. 4.

I may therefore assert it to be a rule, that scales from every part of the body of one and the same individual cod exhibit the same alternations of minima and maxima as regards breadth of the sclerite rings; in other words, that the entire scale covering of any single cod may be characterised by a certain definite number of growth rings.

From the material available, consisting of scales taken from marked cod, it was an easy matter to determine how far these peculiar rings had any relation to annual growth or not; the best specimens in this case were naturally those of fish which had lived for a long period in freedom after being marked. In cases where a year had elapsed between the taking of the two scale samples, the scale curve should then be augmented by a maximum and a minimum; after the lapse of two years, two maxima and two minima should have been formed. This was found to be beyond all question the case, and we have thus succeded in proving that the scales of the cod exhibit growth rings having their origin in an annual periodicity in the growth of the scale. A few scale curves indicating this are here given (Fig. 5); it may be added, that the specimens selected are not hypertypical. Numerous other scales exhibit equally conclusive proof of the statements here advanced (*vide* Figs. 9—10).

Direct examination of cod scales taken at different seasons of the year also confirms, as might be expected, the results already obtained. Cod taken in late summer have as a rule broad sclerites on the outer margin of the scale, whereas the scales of those taken in midwinter are most frequently found to have narrow sclerites at the outer edge. As, however, the scales may sometimes be found to exhibit a kind of secondary or "apparent growth rings" — which will be referred to later on — actual proof can only be afforded by investigations based on experimental methods.

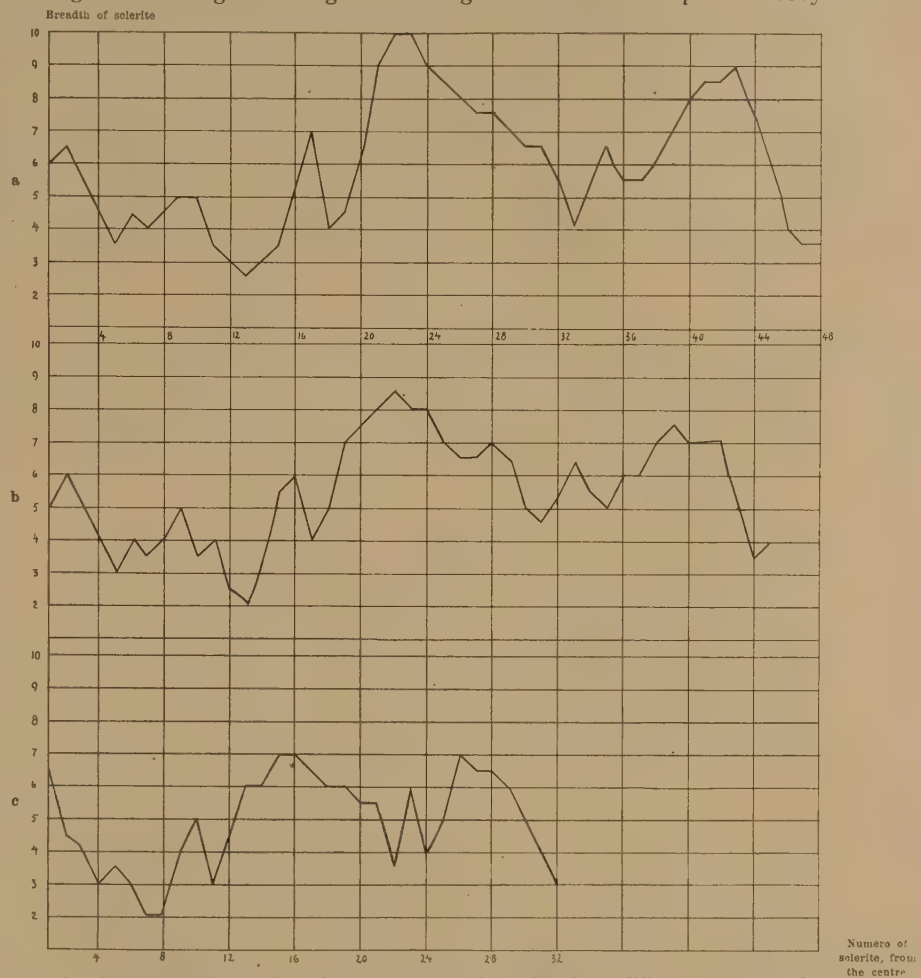


Fig. 4. Curves showing uniformity of structure in scales from different parts of the body. *a.* midway between lateral line and second dorsal fin; *b.* at base of pectoral fins; *c.* dorsal area obliquely in rear of eyes.

It is a known fact that at the Faeroes, the eggs of the cod are laid about 1. April, the young making their appearance at the close of that month, the scale covering, however, being first apparent in summer, in or about the month of August. As the innermost sclerite rings are always relatively broad, we have here a further proof that these broad rings are of summer growth. During the following winter, narrow rings are formed, next summer broad, etc. Repeated observations and combinations of the same have led me to the conclusion that the maxima of the curves fall about the 1. September, the minima during early March. The number of minima in a scale curve thus directly denotes the age of the cod in years: a month should, however, probably be deducted in order to obtain the exact figure for the age of the cod.

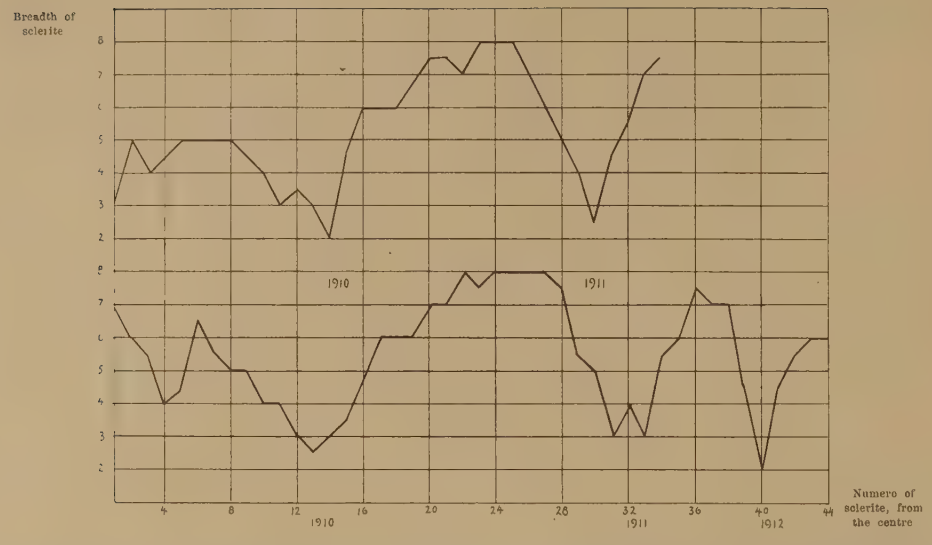


Fig. 5 *a*. Scale curves from capture and recapture of a Faeroe cod, ♂ No. 8777. First caught 28. Aug. 1911 (length 43 cm., weight 800 gr.); recaptured 12. Sept. 1912 (length 50 cm., weight 1440 gr.). In conformity with the fact that the fish has lived one year in a free states, we find one new minimum formed on the scale curve.

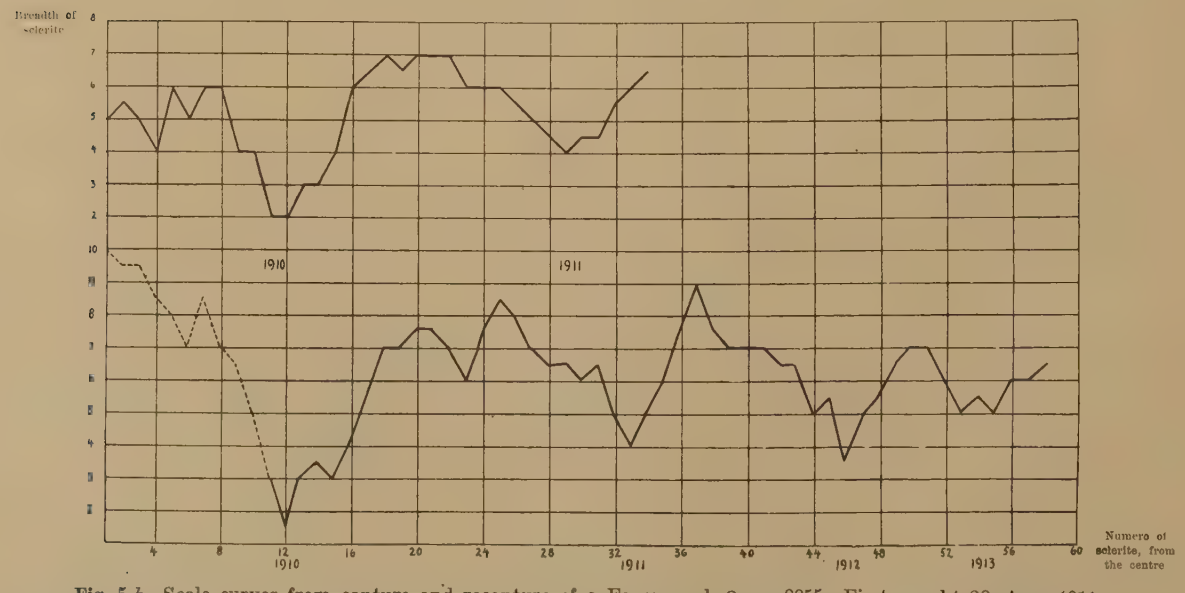


Fig. 5 *b*. Scale curves from capture and recapture of a Faeroe cod, ♀ no. 8855. First caught 28. Aug. 1911, (length 43 cm., weight 800 gr.) recaptured 1 Sept. 1913, (length 66 cm., weight 3300 gr.). Two new minima formed on the scale curve, answering to the two years spent in free state. The dotted portion of the lower curve does not give a true impression of the growth of the normal scale, this being a "regeneration scale".

6. Relation between Growth Increment of the Scales and that of the Cod.

It would seem natural to suppose that the increase in size of the scales is closely related to the growth of the cod; as to the proportion between these two rates of growth, however, nothing can be said with certainty without previous investigation.

In order to elucidate this point, scale samples were taken from cod which had been found to have increased in length in different degrees between marking and recapture. First of all, the developement obtained by the scales at time of capture was determined by microscopical investigation of the separate individuals. In one specimen, for instance, the scales exhibited 2 minima and further, five sclerites of the third year's growth. On recapture, the scales had increased in size. It was here easy to determine the situation of the sclerite ring representing the outermost ring at the time of first capture, and by measuring first the longest radius of the whole scale and thereafter that portion of same which had accrued in the meantime, the proportion between the former and present radius of the scale was easily determined. The length of the cod itself had, moreover, been measured both at time of marking and on recapture, so that it was possible to see whether any direct relation existed between the two increments of growth. Table I shows the respective measurements for the cod, from each of which 7 scales were taken and measured.

Table I.

	Cod I			Cod II			Cod III			Cod IV		
	α	β	α/β	α	β	α/β	α	β	α/β	α	β	α/β
	$^{5}/_{7}$ 1912	$^{22}/_{9}$ 1913		$^{6}/_{7}$ 1912	$^{25}/_{7}$ 1913		$^{17}/_{8}$ 1911	$^{17}/_{10}$ 1912		$^{28}/_{8}$ 1911	$^{1}/_{9}$ 1913	
Length of fish in cm.....	40	55	0,727	31	43	0,721	40	51	0,784	43	66	0,652
Length of radius: scale I..	184	226	0,814	182	250	0,728	285	350	0,814	250	380	0,658
- II..	210	268	0,784	187	262	0,714	220	273	0,806	265	380	0,697
- III..	240	316	0,759	181	254	0,713	270	333	0,811	242	371	0,652
- IV..	232	292	0,795	169	244	0,693	260	322	0,807	253	373	0,678
- V..	164	205	0,800	177	247	0,717	305	365	0,836	158	238	0,664
- VI..	195	236	0,826	168	238	0,706	285	321	0,888	225	332	0,678
- VII..	236	286	0,825	191	266	0,718	255	300	0,850	230	347	0,663
Mean...			0,800			0,713			0,830			0,670

In the table above, α indicates first capture, β recapture. The relation of $\alpha : \beta$ shows, in the first place, that all the scales have increased in approximately the same relative proportion, and further, that the increments of growth in scale and cod respectively are very nearly directly proportional. The deviation from complete proportionality in the four cases here given may be ascertained by working out the following four fractions (Table II), one for each cod, the numerator being the mean of the proportions between the lengths of the scales on capture and recapture, the denominator indicating the proportion between the length of the fish when first caught and its length when recaptured.

Table II.

Cod I	Cod II	Cod III	Cod IV
$\frac{0.800}{0.727} = 1.10$	$\frac{0.713}{0.721} = 0.99$	$\frac{0.830}{0.784} = 1.06$	$\frac{0.670}{0.652} = 1.03.$

Had the relation been absolutely proportional in all cases, each of these values would have been = 1. It would thus appear that the scales have on the whole increased somewhat less in size than should be the

case if perfect proportion existed; the discrepancy, however, being but slight, and the measuring of live cod being subject to considerable inaccuracy, it would seem highly probable that the relation really is a proportional one.

From this it follows, that the position of the winter rings in a scale affords a means of calculating, with a very considerable degree of accuracy, the annual increment of growth of a cod for each separate year since hatching.

Taking these two facts together; that broad sclerites are formed during summer, narrow in winter, and that the growth increment of the scales is directly proportional to the increase in length of the cod, we can thence, I think conclude, that cod from the Faeroes, — and probably also from other localities, — grow most in summer. This theory — that broad sclerite rings indicate rapid growth — is supported by a fact immediately noticeable on examining the growing marginal zone of the scales. The rule is, that only one sclerite ring is formed at a time. The penultimate is always as completely formed as those nearer the centre. Fig. 6 illustrates this: *a* = "mature" sclerites, *b* the outermost, imperfectly developed sclerite ring, beyond which lies the margin, *c*, of the basal lamella of the scale above referred to. This portion generally projects somewhat beyond the outermost sclerite ring, as a transparent border, and forms the base on which new sclerites will subsequently be formed. Having in mind the fact that only one sclerite ring is formed at a time, it will seem only natural that large sclerite rings should be associated with rapid growth, and *vice versa*, since the scale would, during a period of rapid increase in the length of the fish, necessarily form a broad border to its basal surface, in order to keep pace with the developement of the whole body, The sclerite ring subsequently formed, having the broad border as its base, will naturally likewise be broad, as only one sclerite ring is formed when the one within the margin has matured. Similarly, small sclerites will be formed when the growth of the fish is slight.

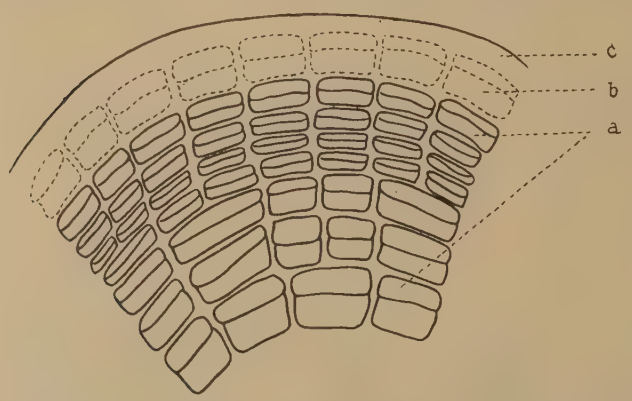


Fig. 6. Margin of cod scale, surface view. *a*, mature sclerites; *b*, outermost sclerites in process of formation; *c*, margin of basal lamella of the scale.

The word "mature" which occurs in the foregoing in connection with the sclerite rings, I have used advisedly; as the growth of the sclerites and the scale is never completed. The scleroblast strata are constantly depositing material on the upper and lower layers of the scale, so that the sclerites, and the scale itself, continue to increase in thickness throughout the whole life of the cod. This may be easily seen by measuring the thickness of older and younger scales with a cover glass measure. Without going into details on this point, it will suffice to mention that the scales of a large cod may often be four times as thick as those of a small specimen.

7. Influence of External Conditions on the Course of the Scale Curves, and thus on the Growth of the Cod.

On examining a number of cod from a certain locality it will be noticed that the curves exhibit, on the whole, a considerable similarity. This may be immediately presumed to be due either to certain racial peculiarities in the material in question, or to the fact that the external conditions, which may be supposed to be more or less homogeneous within a narrowly restricted area of sea, have distinctly affected all the individuals during ontogenesis. We have, moreover, a means of ascertaining which is the decisive factor.

The scale samples from the Faeroes included, as it happened, several taken from cod which had been caught simultaneously both in the first and second instance. Thus on the 16th of August 1911 six cod were taken, all of which were simultaneously recaptured nine months later at the same spot. Of these, three fish of approximately the same size were selected; their weights and length at time of capture and recapture will be found in the table below:

Table III.

	First capture, 16/8 1911		Recapture, 17/5 1912 (8422 25/5 1912)	
	Length (cm.)	Weight (gr.)	Length (cm.)	Weight (gr.)
♂ Cod No. 8437	38	625	52	1400
♀ - - 8422	43	800	56	1725
♀ - - 8440	41	725	51	1375

It will be noticed that both sexes are represented, and that the absolute increment of growth is somewhat different. Since the fish were taken together both at the beginning and end of this period of nine months, it may be supposed that they have lived throughout that time at the same place, and been subjected to very similar external conditions, since the temperature and salinity of the water, its supply of nourishment, light, and many other factors must have been the same for all individuals. It will moreover be reasonable to argue that since the fish have lived in company during these nine months, they will probably also have lived not far apart during the time previous to their first capture. All these things considered, it appeared to me possible, that a comparison of the scale structure in these three fish might lead to some conclusion as regards the influence of external conditions on the same.

By way of experiment, the following method was tried, and proved satisfactory: Five scales of each of the three cod were taken from the recapture samples (i. e. from 1912). The breadth of some 25 of the outermost sclerite rings was measured in the usual manner, this corresponding approximately to the increment of growth for the last two years, and partial scale curves drawn accordingly for each fish. It was then found that these curves were very similar in all three cases, as much so as even to include peculiar deviations in the course of the curves, a characteristic secondary minimum for the summer of 1911 being apparent in all the curves (Fig. 7). The scales had, moreover, formed the same number of sclerite rings during the period in question, or the difference was in any case so slight, as to permit of the comparison shown in Table IV, by means

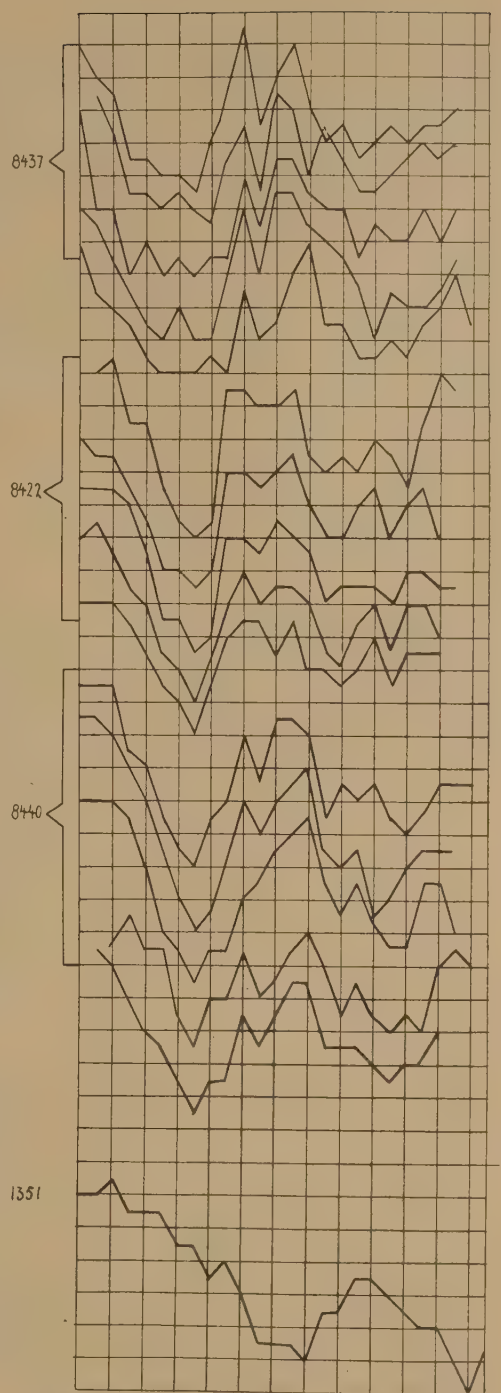


Fig. 7. Five partial scale curves (of abt. 25 outermost sclerite rings) of each of the three Faeroe cod found living together: ♂ No. 8437, ♀ No. 8422, ♀ Nr. 8440, showing uniformity in the course of the scales. — Below, corresponding curve for another cod, ♀ No. 1351, locality 6—8 nautical miles distant from the above. (Taken 1. Juli 1912, length 58 cm., weight 1700 gr.). The curve for the 25 outermost sclerite rings here presents a different appearance.

Table IV.

Cod Nr. 8437	8	7	6½	4½	4½	4	4	3½	5	6½	8½	5½	7	8	6	5	5½	4½	5	5½	5	5½	5½	6	Scale I
	8½	8	7	5	5	4½	5	4½	4	6	7	5	8	7½	5½	7	6	5	5	5½	6	6½	6	6½	— II
	9½	6½	6½	4½	5½	4½	5	4½	5	5	7½	6	8	8	7	6½	6½	5	6	5½	5½	6½	5½	6½	— III
	8	7½	6½	5½	4½	4	5	4	4	6	8	6	8½	8½	7½	7	6½	5½	4	5½	5	5	5½	6½	— IV
	9	7½	7	6½	5½	5	5	5	5½	5	7½	6	6½	8	9	6½	6½	5½	5½	6	5½	6½	7	8	— V
	43	36½	33½	26	25	22	24	21½	23½	28½	38½	28½	38	40	35	32	31	25½	25½	28	27	30	29½	33½	Mean
Cod Nr. 8422	7½	7½	8	6	6	4	3	2½	3	7	7	6½	6½	7	5	4½	5	4½	5½	5	4	6	7½	7?	Scale I
	7½	7	7	6	5	3½	3½	3	3½	6½	6½	6	6½	7	5½	4½	4½	5½	6	4½	5½	6	4½		— II
	8	8	8	7½	6	4	4	3	3½	6½	6½	6	7	6½	6	4½	5	5	5	4½	5½	5½	5	5	— III
	8	8½	7½	6½	6	4½	4	3	4½	6	7	6	6½	6½	6	4½	4	5½	6	4½	6	6	5	5	— IV
	6½	6½	6½	6	5	4	3½	2½	4	5½	6	6	5	6	4½	4½	4	4½	5½	4	5	5	5		— V
	37½	37½	37	32	28	20	18	14	18½	31½	33	30½	31½	33	27	22½	22½	25	28	22½	26	28½	27		Mean
Cod Nr. 8440	9	9	9	7	6½	5	4	3½	5	5½	7½	6	8	8	7½	5	6	5½	6	5	4½	5	6	6	Scale I
	10	10	9½	8½	7½	6	4½	3½	4	5½	7½	6½	7½	8	8½	6	5½	6	4	4½	5½	6	6	6	II
	9	9	9	8½	7	5	4½	3½	4½	4½	6	6½	7½	8	8½	6½	5½	6½	5½	4½	4½	6½	6½	5	— III
		c. 8	7	8	7	7	5	4	5½	5½	7	5½	6	7	7½	6½	5	6	5	4½	5	4½	6½	7	— IV
		8½	8	7	6	5½	4½	3½	4½	4½	6½	5½	6½	7½	7½	5	5	5	4½	4	4½	4½	5½	5½	— V
		c. 44½	42½	39	34	28½	22½	18	23½	25½	34½	30	35½	38½	37½	29	27	29	25	22½	24	26½	30½	29½	Mean

of which a "mean scale" for each fish could be constructed. In this table, all the measurements of breadth for the five scales from each fish are placed in perpendicular columns in such a manner that figures in the same column give the measurements of sclerites corresponding one to the other. By adding up values in these columns, we obtain a "mean scale" for each cod. These curves of the abstract "mean scales" (Fig. 8) are perhaps somewhat less characteristic in detail than the individual curves; the similarity which they do exhibit in the main features is, however, an indisputable proof of the fact that cod living under the same conditions obtain scale curves similarly formed, provided the fish themselves are sufficiently alike in age and size to render them reasonably comparable. — The scale curve will to a certain extent afford a graphical illustration of the varying conditions, favourable or not, under which the cod have lived, each scale being, so to speak, an automatic register.

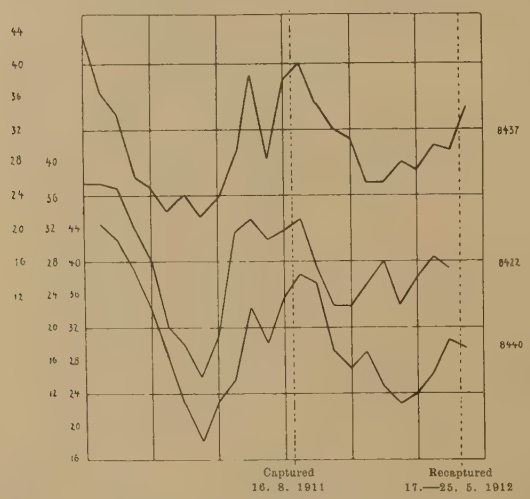


Fig. 8. "Mean scale" curves for the three companion fish.

It would be out of place here to discuss the question of racial peculiarity as a cause of the similarity in the course of the curves for the three fish. The fact that the cod are of the same race, possibly even the same parentage, would certainly serve to render the material comparable, but is insufficient to explain the great similarity in the growth of the scales from the second to the fourth year in the life of the fish. It might be imagined that spawning possibly could involve so great physiological changes as to leave some distinctive and constant mark on the scales; the fish here in question however, were not mature during the period of investigation, so that this possible factor may be entirely disregarded.

A comparison of the scale curves for these three cod with those for other fish which had lived for the same period of time at other localities at the Faeroes immediately shows that even when the individuals from such other localities are more or less comparable in point of age and size with the first, there is no

similarity in the scale curves beyond such annual periodic increase and decrease in breadth of the sclerite rings as may be noted in the case of all cod. An illustration of this will be found in Fig. 7, where, in addition to the 15 uniform curves, another has been added below, this being that of a cod comparable in point of age and size with the other three, but taken from another locality. It will be noticed, that the 25 outermost sclerite rings here produce a different curve. This shows, that even in a so restricted water as that of the Faeroes, there is a probable variation in external conditions.

8. The Typical Scale Curve. Secundary Minima.

After having had under observation a number of scale curves from a locality such as the Faeroes, it will be found that despite the many minor variations in the course of the curves, certain features will yet

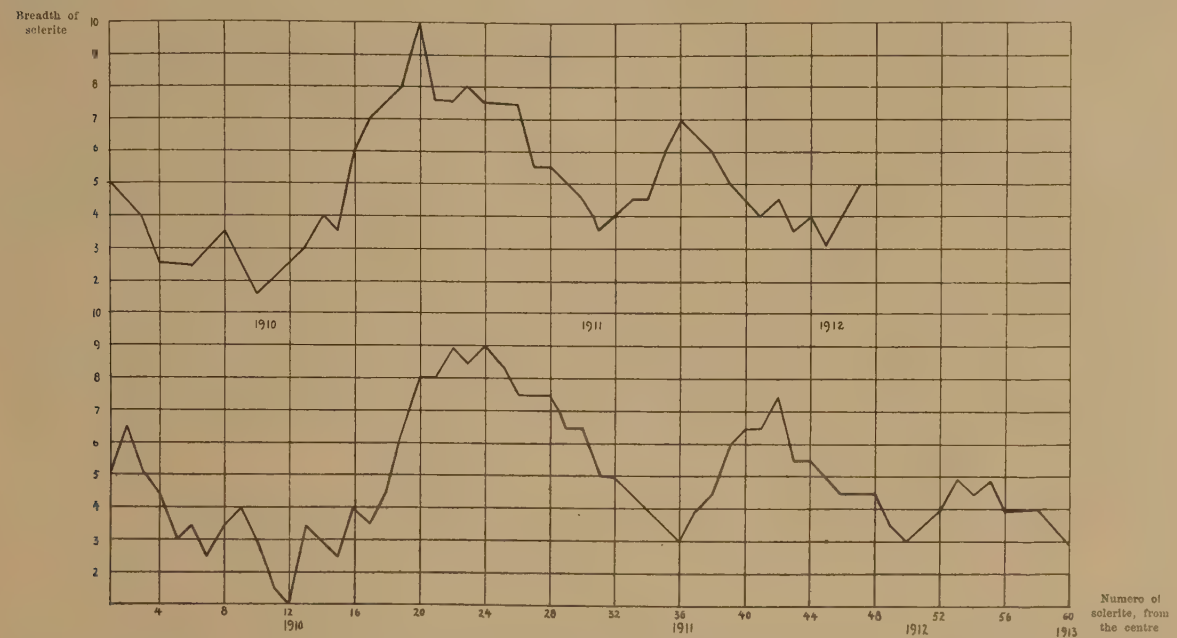


Fig. 9. Typical scale curves of a Faeroe cod (♀ No. 1761). First caught 2. July 1912 (length 48 cm., weight 1150 gr.). Recaptured 17. Febr. 1913 (length 60 cm., weight 2150 gr.).

remain which are common to all. The Faeroe cod, for instance, generally form about 12 sclerite rings during the first year of life, 19 in the next, 11 in the third, 7 in the fourth, 6 in the fifth, etc. Even though several curves may exhibit somewhat different values in this respect, the increase in number of scale rings during the first years of life as given above may be regarded as the normal, as I have found by countings with 100 scales of different specimens of cod taken at different times and places. It is also a characteristic feature, that the curves have a tendency to approach the *m*-form (in contrast to the *u*) and finally, the variation in the breadth of the sclerite rings decreases continually, the curve falling somewhat during the later years, i. e. the sclerites grow narrower and more uniform from year to year. Fig. 9 shows one such typical curve for a Faeroe cod.

In seeking to ascertain the age of any particular cod, it is important to have some previous acquaintance with the general appearance of the scale curves. These may, as already mentioned frequently exhibit peculiar, more or less pronounced minima, not representing any winter, but having their origin in some unfavourable

period in the life of the fish, e. g. times of sickness, cold, or lack of food. These secondary minima can of course make their appearance at any point in the course of the curve, and can generally be recognized as such, especially with some previous experience as to the normal appearance of these curves.

Fig. 10 shows, by way of example, a curve containing a secondary minimum, which is immediately discoverable from its position, falling as it does almost in the most favourable period of growth. Figs. 7 and 8 afford similar illustrations.

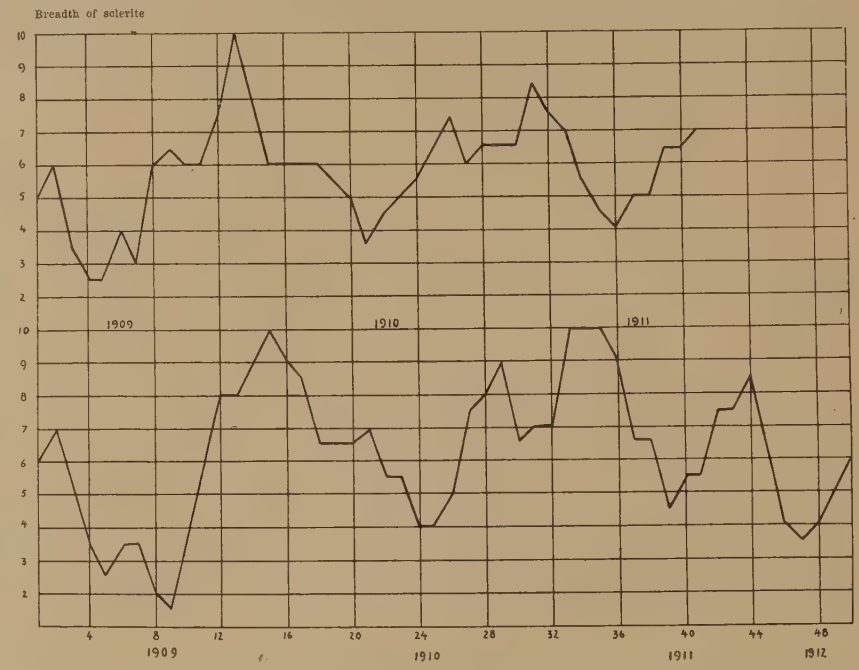


Fig. 10. Scale curves (of Faeroe cod, ♂ Nr. 8882) with typical secondary minima, two small in second growth zone, one in third. First caught 28. Aug. 1911 (length 52 cm., weight 1400 gr.); recaptured 6. Juli 1912, (length 60 cm., weight 1805 gr.).

Greater difficulty is experienced in determining the age of comparatively old fish. As already mentioned, the scale curve — for Faeroe cod — exhibits, with increasing age of the fish, maxima and minima of continually less pronounced character, whereby the risk of confusion between secondary minima and winter rings is increased. In most cases, there will be no possibility of doubt; there will, however, more often be grounds for hesitation in determining the age of cod over 4 years old than in the case of younger fish. This will be of no very great importance in practical work, inasmuch as there will generally be more occasion to determine the age of younger than of

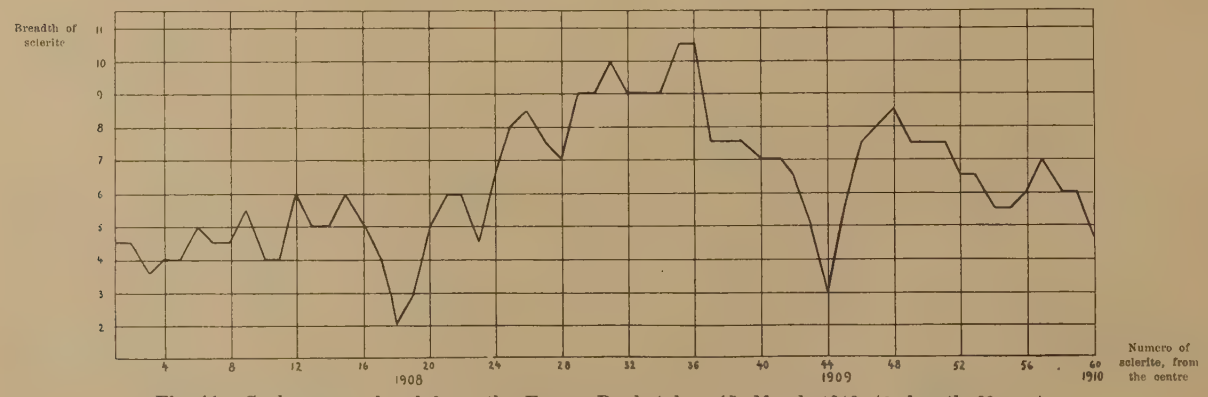


Fig. 11. Scale curve of cod from the Faeroe Bank taken 15. March 1910, (♀, length 68 cm.).

older fish; moreover, cod from other localities than the Faeroes exhibit as a rule far more distinct growth rings — even in the case of very old fish — than is the case in this particular water.

For purposes of comparison with the Faeroe coast cod, I have included here a curve for a cod from the Faero Bank, which lies some 50 miles S. W. of the nearest land, Suderö (Fig. 11). The bank is separated

from Suderö by deep water, the bank itself rarely reaching to within 50 fathoms of the surface. The cod spawn on the spot, and live here under conditions which, if only on account of the greater depth, must be far different from those under which the coast cod thrive. Apart from the possibility that a distinct race may have developed here, the scale curves at any rate exhibit a distinct difference from those of the coast cod. The growth is, as will be seen, enormously strong during the first few years.

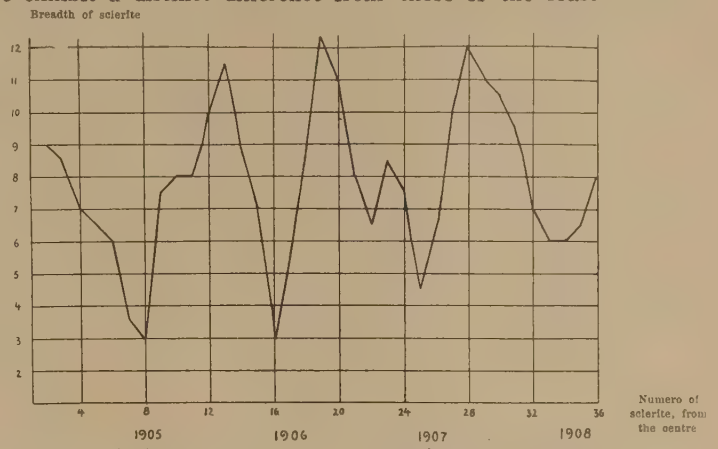


Fig. 12. Scale curve of cod from E. Iceland (Seyðisfjord), taken 31. July 1908 (♀, length 43 cm.).

Iceland cod again exhibit curves of an entirely different form, — at any rate, on the east coast, which is washed by the East Icelandic Polar current, and where the temperature in consequence is far lower. The growth of the cod is far inferior, and the curve is marked by extremely pronounced maxima and minima. By way of example, a curve is also here included as being typical for the locality (Fig. 12). The scale itself, on which the curve in question is based, is shown in Fig. 3 on the Plate. On the west coasts we find conditions far more resembling those of the Faeroes, the Atlantic current in both cases occasioning a milder temperature. The curves for the west coast cod also largely resemble those characteristic for the Faeroes. Another curve here given would seem to suggest that the fish in question, which was taken on the east coast, had lived during its first years of life in west coast waters, subsequently migrating to the less favourable conditions at the east coast, where its growth was then retarded during the succeeding years (Fig. 13).

Cod from the Baltic may likewise furnish curves having an entirely different aspect. Fig. 14 shows a highly characteristic scale curve, the fish in question having evidently grown slowly, but very regularly

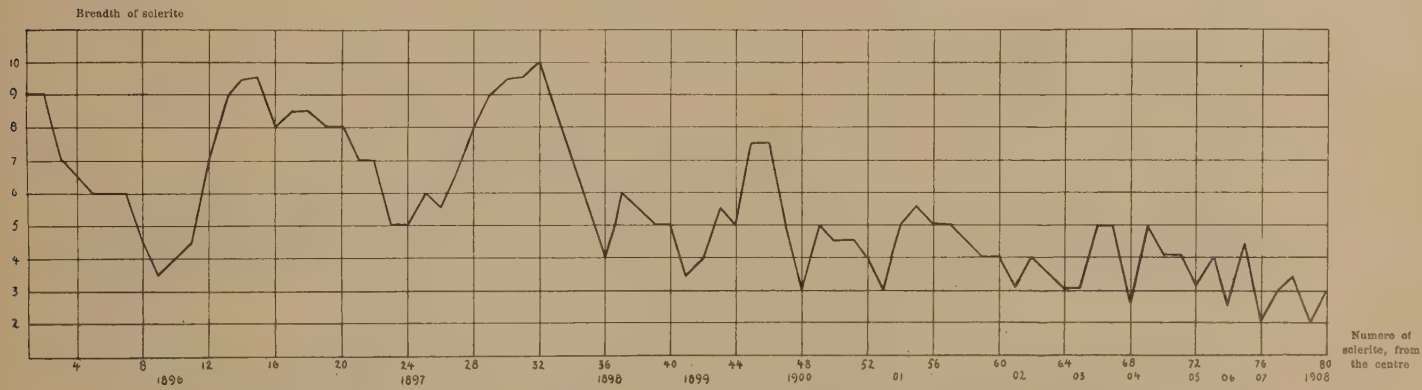


Fig. 13. Scale curve of cod (♀, length 118 cm.) from E. Iceland, showing 13 distinct minima. Taken 28. July 1908. Shows fairly good growth for the first 3 years, then suddenly decreasing for the remainder. — It should be noted that the dates of the years under this curve may possibly be incorrect, as the otoliths (*vide infra*) seem to indicate that 1 more minimum should have been formed, in which case it should probably fall between those marked 01 and 02.

year for year. This peculiar curve would seem to indicate that we have here to deal with a distinct race, probably the Baltic dwarf race.

Having in mind the scale curves from the cold East Iceland waters, it would seem probable that the periodical annual alternation between rapid and less rapid growth in the cod is directly or indirectly connected with the change of temperature. The records of surface temperature from the Faeroes do, as a

Table V. Surface temperatures, mean figures for the years 1891—1900, calculated from daily observations.

	Jan.	Febr.	March	April	May	June	July	August	Sept.	Oct.	Nov.	Decbr.
Thorshavn (Faeroes).	5°,6	5°,4	5°,5	6°,6	7°,7	9°,3	10°,4	10°,6	10°,2	8°,8	7°,7	6°,5

matter of fact, tend in this direction, as will be seen from Table V[1]. It will be seen that the warmest period coincides very closely with the season at which the growth of the cod is most rapid, the coldest with that

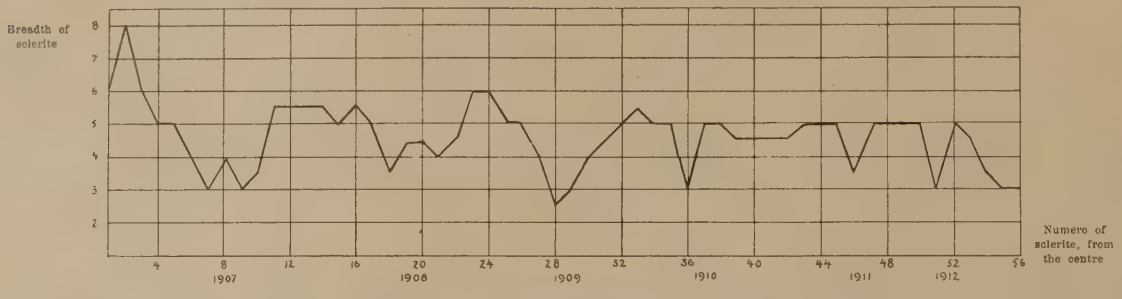


Fig. 14. Scale curve of cod (ripe ♀, length 43 cm.) from Copenhagen. Presumably belonging to the Baltic dwarf race. Taken 5. Nov. 1912.

when growth is slower. Everything seems to indicate that the rate of growth of the cod is highly dependent upon the conditions of temperature in the water, although perhaps in the main indirectly, through the effect of temperature upon the quantity of nourishment.

9. Investigation of Otoliths.

The growth zones of the scales were, as we have seen, easily amenable to very accurate measurement with the micrometer, owing to their peculiar cellular structure. No such structure is, however, apparent in the case of the otoliths, and it was necessary therefore to have recourse to other means in order to determine whether these also were subject to annual periodical growth.

The otoliths of the cod are almost almond shaped, dentate, somewhat twisted and irregularly curved; the length, in fish of "medium size", being 1—2 cm. A merely macroscopic observation of these objects in transmitted light will be sufficient to reveal a series of concentric rings, some light, some dark. By filing down, these rings are rendered more distinctly visible, and with the aid of a lens or microscope it will be seen that the whole of the otolith is built up of fine concentric calcareous strata, which on closer scrutiny are found to divide up into a series of lamellæ, increasing in number as they diminish in thickness, and with no sharply defined limits. The growth rings are produced by the alternation of more and less transparent zones. The zones which appear lighter in transmitted light will thus naturally produce a darker effect in reflected light, and vice versa.

[1] From: Johs. Schmidt: Fiskeriundersøgelser ved Island og Færøerne, (Skrifter udgivne af Kommissionen for Havundersøgelser, Nr. 1, 1904).

In order to ascertain with certainty how far there might here again be question of growth rings, I subjected to careful examination a number of otoliths taken from cod, the age of which I had previously determined from investigation of the scales according to the graphical method above described. For this purpose I found it necessary to grind down the otoliths, in order to bring out all peculiarities in the closest detail. The method was as follows:

An otolith was broken across in the centre, and the broken surface of the one half ground on an ordinary rotary grindstone of fine grain, which was kept well moistened. As soon as a smooth surface was formed, this was further treated on an extremely fine oilstone with a few drops of paraffin oil. This gave a good clean surface, but as yet unpolished. Finally, therefore, the polishing was done on a leather strop, treated with oil and ferric oxide. The surface was now perfectly polished, and the stone, after being rinsed in xylol and wiped with chamois leather, was gummed to the object glass as follows: A drop of xylol-Canada balsam was placed on a clean object glass near the one end, and the polished sectional surface of the otolith pressed through the balsam flat down upon the glass. The preparation was then left overnight in a thermostat to dry, and grinding recommenced next day from the other side. Here likewise the rotary grindstone was first called into play, until the preparation had reached a thickness of abt. $^3/_4$ mm. By means of the grinding and polishing methods already described, the thickness was then reduced to between 0.2 and 0.1 mm. The first attempts resulted in the breaking of a number of the preparations owing to the somewhat rough usage; in a short time, however, one becomes sufficiently practised to avoid this. When the surface was finally polished, the surrounding Canada balsam was washed off in xylol by means of a small, soft brush, care being taken to avoid dissolving the very fine layer of balsam beneath. After all superfluous balsam had been removed, a little dark wax was melted, and a thin layer of this placed all round the otolith with the aid of a match. In order to ensure the exact adhesion of the wax to the otolith, the preparation was slightly warmed by being passed several times over a flame; as the wax melted, it flowed in naturally close up to all sides of the otolith, which then, in transmitted light, showed up beautifully clear against the dark ground. If the layer of balsam beneath happens by any mischance to become partially dissolved, then the melted wax will flow in under the stone and disturb the view. As soon as the wax had set, a drop of xylol-Canada balsam was placed on the surface of the otolith, and a cover glass laid over it and pressed down. The whole of the space beneath the cover glass was then filled with xylol-Canada balsam, and the preparation left to dry overnight. Thus treated, the otolith was excellently adapted to microphotography, whereas without the surrounding wax, it proved too dark, with too great refraction at the edges, occasioning a kind of a halo on the negative. The microphotographs distinctly showed the lighter and darker zones.

Even a more direct examination of the growth rings in the otoliths seemed to suggest that these exactly corresponded to those found in the scales. The more precise method here described furnished conclusive proof of this. By way of example, I reproduce here some curves of cod scales, together with microphotographs of the corresponding otoliths. From these it is distinctly evident that the otoliths in transmitted light reveal exactly the same number of lighter zones as there are minima in the scales. In other words, the otoliths exhibit growth rings, and the zones which here appear of lighter hue are those formed during winter.

The oldest cod which I have had an opportunity of examining I estimated from the scales as being $13^1/_2$ years old (*vide* Fig. 13). In my subsequent investigations of otoliths, it occurred to me to see what appearance those of this fish would present. The result will be seen in Fig. 4 on the Plate. Judging from the otolith, the fish would rather appear to be a year older, (14—15 years); having in mind, however, the increased uncertainty of the scale method already referred to when dealing with older specimens, the two results appear to me to be sufficiently close. It should be noted, moreover, that scale and otolith both agree in exhibiting fairly rapid growth during the first three years, when a sudden reduction of the rate appears, extending over the years following.

Fig. 5 on the Plate shows 4 winter rings in an otolith taken from the Iceland cod of which a scale is shown in Fig. 3 on the Plate. The scale curve, (Text Fig. 12) shows that the scales have likewise 4 winter rings.

Also in the otoliths we may find secondary minima, i. e. faint or narrow light zones, which do not indicate winter growth, but evidently correspond to the secondary minima in the scales, referred to in the foregoing. In order to illustrate this, I ground down two otoliths of two cod which exhibited typical secondary minima in their scale curves. A scale curve of one of them will be seen in Fig. 10, and a ground preparation of an otolith from the same fish is shown in Plate Fig. 6 where we find, though not particularly distinct, yet still indubitably visible[1], two secondary minima — light zones — between the first and second winter rings, with a minimum more faintly apparent between the second and third.

It is thus evident, that in the cod examined a very high degree of uniformity exists between the growth of the scales and that of the otoliths. Both scales and otoliths exhibit growth rings by means of which the age of the cod can be determined.

10. The Practical Utility of the Scale Method.

The exact investigation of otoliths being, as has been seen, a lengthy and difficult business, this method will, in age determinations, naturally only be employed in cases of doubt. Even with younger fish, it is no easy matter to distinguish between true and apparent growth rings by superficial examination.

It is difficult to make any general statement as to the degree of certainty with which determinations of age can be made by the scale method. My experience hitherto leads me to believe that the locality from which the fish are taken is a factor of the highest importance here. In certain waters, the growth rings are outlined with extreme distinctness in the scales; in others, they are less distinct. Having learned something of the great influence exerted by external conditions on the course of the scale curves, it would be natural to suppose that the growth rings would be most distinct in waters where the difference in temperature between summer and winter was greatest, and *vice versa.* This, however, I do not believe to be the case. My reason for adopting this view is, that I have found the growth rings to be far more distinctly marked in cod from the east coast of Iceland than in those from our Danish waters, despite the fact that the difference between winter and summer temperature of the water is far greater here than off the coasts of Iceland. We have doubtless here to deal with other factors, probably racial peculiarities, which are not so easily determined.

Another important point in age determinations is the question as to whether the fish are young or old. Naturally, it will be easier to determine the age of young fish, and when the normal growth rate of the cod decreases considerably with increasing age, as is the case with fish from the Faeroes, this will render it especially difficult to deal with older specimens. At places where the annual increment of growth is more regular from year to year, there does not appear to be any age limit in this respect.

In order to give a somewhat correct impression as to the practicability of the method when dealing with cod from the Faeroes, which appear to be relatively difficult material when over 3—4 years old, I may mention that I found in 87 % easily determinable by examination of only 1—2 scales from each fish: in 10 % of cases there was some doubt as to whether the cod might be a year older — or younger — than estimated, (all these were over 3 years old), while in 3 % of cases no decision was possible.

[1] Fig. 6 on the Plate has lost something of its original distinctness in the process of reproduction. The author is in possession of the original microphotographs which show the secondary minima plainly.

It will take an operator with some practice in measurement work about 15 minutes to note down the scale measurements of a medium sized cod, say 50—60 cm., this time including preparation. If the special paper for the graphs has previously been placed ready to hand, it will be a matter of a couple of minutes only to draw the curve. This will serve to give an idea as to the practical use of the method as far as concerns the time required. In many cases it will be possible to arrive at a determination of age without making exact measurements, as it will suffice to note, by mere microscopic observation, the number of minima visible in the scale. When using this easier method, however, it will hardly be possible to avoid occasionally confusing secondary minima with true winter rings. It is also a great help in comparative studies of this nature to have before one curves of the material already dealt with. Increased familiarity with these curves enables the operator to perceive various features not immediately apparent at first sight.

Notes to the Plate.

All the figures are from microphotographs, not retouched.

Fig. 1. Scale of Faeroe cod (♂, No. 1622) on first capture, 6. July 1912 (length 34 cm., weight 400 gr.).

Fig. 2. Scale of same on recapture, 13. May 1913 (length 46 cm., weight 980 gr.).

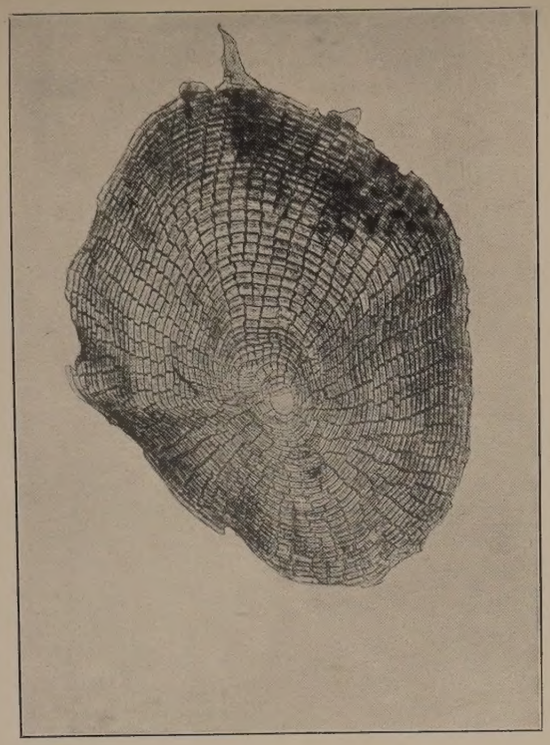
Fig. 3. Scale of cod (♀) from E. Iceland (Seyðisfjord). Taken 31. July 1908 (length 43 cm.). Scale curve shown in Text Fig. 12, p. 17. Cf. also Fig. 5 in this plate.

Fig. 4. Otolith of cod from E. Iceland (♀, length 118 cm.). Taken 28. July 1908, About 14 light winter zones visible Cf. scale curve of same fish, Text Fig. 13, p. 17. — × $^{25}/_{1}$.

Fig. 5. Otolith, with 4 winter zones, of cod (♀) from E. Iceland (Seyðisfjord). Taken 31. July 1908 (length 43 cm.). — Cf. Text Fig. 12, p. 17, and Fig. 3 in this plate. — × $^{23}/_{1}$.

Fig. 6. Otolith (of Faeroe cod, ♂, No. 8882) with secondary minima, two in second growth ring, one in third. Captured 6. July 1912 (length 60 cm., weight 1805 gr.). Cf. scale curve of same fish, Text Fig. 10, p. 16. — × $^{23}/_{1}$.

22. 3. 1915.



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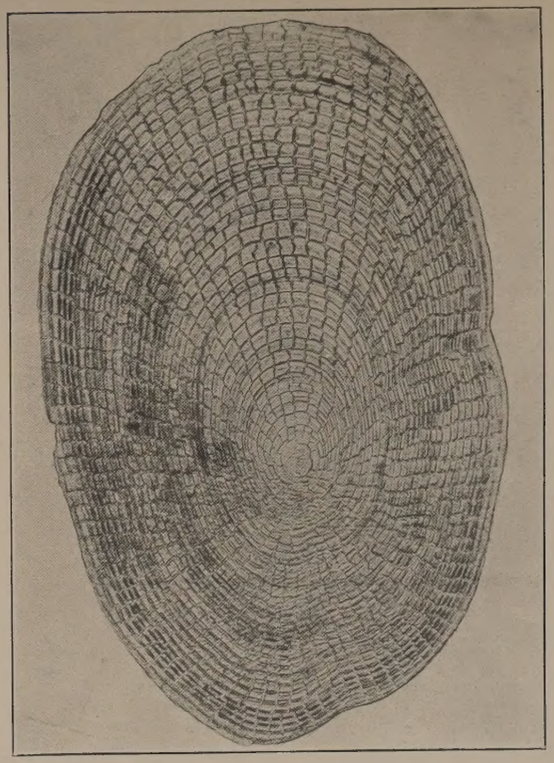

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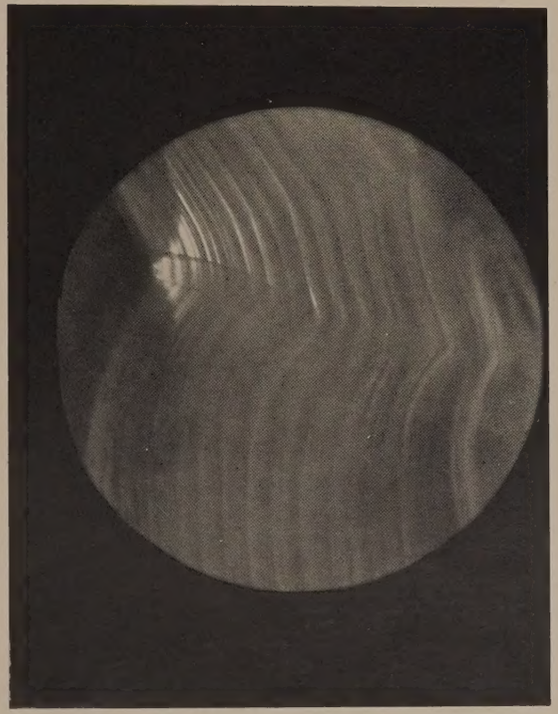

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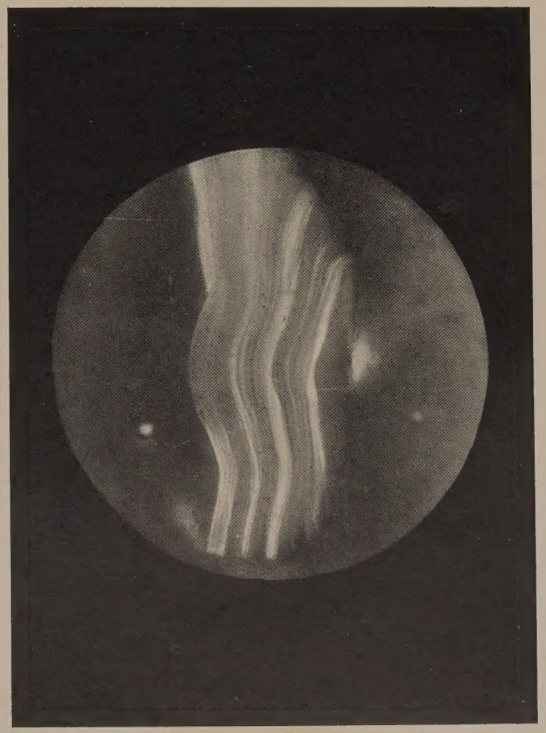

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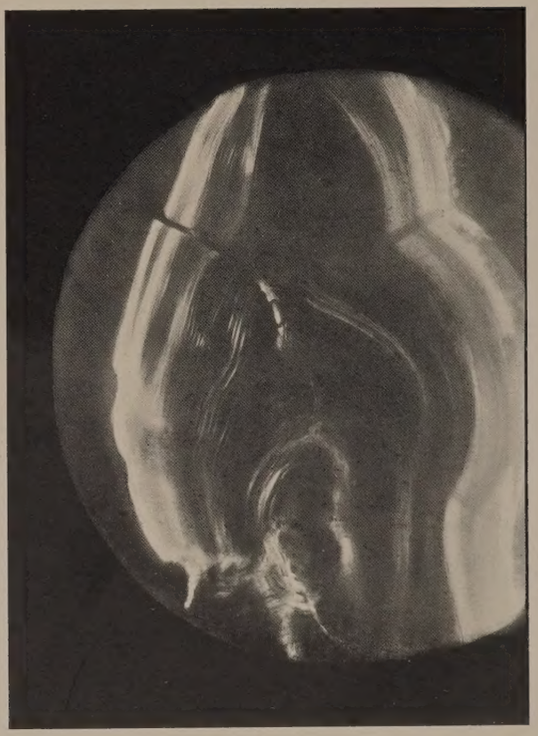

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